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Rare rejection and incomplete responses to experimental eggs in a colonial bird

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Egg recognition has been well studied in brood-parasitic systems, yet its occurrence and function remain poorly understood in colonial species that experience little or no parasitism. We examined egg recognition in the little egret (*Egretta garzetta*), a colonial waterbird in which brood parasitism appears to be rare. We experimentally introduced conspecific, white-breasted waterhen (*Amaurornis phoenicurus*), and quail (*Coturnix japonica*) eggs into egret nests (n = 141) and tested the effects of clutch size, breeding stage, and parental presence on egg recognition. Rejection occurred in only four nests (2.8%) and was restricted to quail eggs, which were substantially smaller and visually dissimilar to host eggs. All conspecific and waterhen eggs were accepted. Rejection involved shell damage consistent with pecking or grasping attempts, but no eggs were completely removed. Females that showed rejection did not differ in egg size from non-rejectors. The Bayesian-regularized logistic model estimates indicated an inverse relationship between egg size relative to the host and the probability of rejection, although credible intervals were wide due to the rarity of events. Several predictors, including clutch size, breeding stage, parental presence, and year, showed highly uncertain effects. Although rejection appeared more common in larger clutches, model estimates did not support a clutch-size effect, likely due to rare events and uneven sampling. Overall, the recognition of foreign eggs by little egrets was poor. In the absence of brood parasitism and low frequency of egg rejection, interactions with dissimilar eggs may be more consistent with generalized nest sanitation or responses to anomalous objects than evolved antiparasitic discrimination.

1. Introduction

Many bird species have developed sophisticated egg detection mechanisms (Peer 2006, Liang *et al.* 2016, Lawson *et al.* 2021). Four main ecological contexts have been identified that may

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favor rejection of foreign eggs: (1) nesting in dense colonies, where individuals may confuse their own eggs with those of neighbors (Lengagne *et al.* 2004, Liu *et al.* 2019); (2) conspecific brood parasitism (CBP) (Lyon 1993, Lyon & Eadie 2008); (3) nest usurpation (Lindell 1996, Peer & Bollinger 1998); and (4) interspecific brood parasitism (IBP) (Soler 2014a, b, but see Samaš *et al.* 2014). Interactions involving interspecific brood parasitism are widely regarded as an important selective force driving the evolution of egg-recognition and rejection behaviors in birds (Stoddard & Hauber 2017, Ruiz-Raya *et al.* 2019). Compared with discrimination of parasitic nestlings, rejection of foreign eggs is a more widespread and effective defense against interspecific brood parasitism (Davies 2011, Soler 2014a, Yang *et al.* 2019), as only a limited number of bird species have been shown to discriminate between their own and foreign nestlings (Grim *et al.* 2003, Grim 2006, Langmore *et al.* 2003, 2009, Sato *et al.* 2010, Tokue and Ueda 2010, Yang *et al.* 2015a, Huo *et al.* 2018, Liu *et al.* 2023).

Other ecological and social factors may also have played a part in the evolution of egg and nestling rejection behavior, apart from interspecific brood parasitism. The first and foremost driver is conspecific brood parasitism (CBP), which has exerted selective pressure on other species to evolve egg recognition mechanisms, especially in the family *Ploceidae* (Lahti & Lahti 2002, Lahti 2006). Other selective contexts include nest usurpation, as observed in mourning doves (*Zenaida macroura*), where hosts may then eject eggs laid by other females (Peer & Bollinger 1998), and high densities of breeding parents that increase the chance of foreign eggs being laid in nests. Empirical evidence for such adaptive responses is mixed across taxa. For example, egg or chick recognition has been documented in species such as song thrushes (*Turdus philomelos*) (Samaš *et al.* 2014), house sparrows (*Passer domesticus*) (Soler *et al.* 2011, but see Yang *et al.* 2015b, Manna *et al.* 2017), russet sparrows (*Passer cinnamomeus*) (Huo *et al.* 2018), spotless starlings (*Sturnus unicolor*) (Liénard *et al.* 2025), and the American coot (*Fulica americana*) (Lyon 2007, Lyon *et al.* 2015), where CBP is a major selective pressure. Brood parasitism in *Ardeidae* might be more common than expected if we consider many of their characteristics that seem to favor the evolution of brood parasitism (Hamilton & Orians 1965, Yom-Tov 1980, Rohwer & Freeman 1989). Factors include synchronous and overlapping breeding schedules, easy accessibility of nests, presence of closely related sympatric species that may act as potential hosts, and high levels of parental care that could enhance the cost–benefit ratio in favor of parasitism (González-Martín & Ruiz 1996). In addition, similarity between parasitic chicks and host offspring may enhance acceptance, while the presence of non-breeding ("floater") females and extra-pair copulations may further increase opportunities for parasitic laying (González-Martín & Ruiz 1996). Together, these ecological and life-history traits suggest that *Ardeidae* may provide favorable conditions for both brood parasitism and the evolution of corresponding antiparasitic defenses.

However, empirical studies have reported considerable variation in recognition abilities among colonial bird species (Liu *et al.* 2019). Studies on egg recognition in colonial nesting birds are sparse, and the outcomes are contradictory. Lanier (1982) observed pinyon jays (*Gymnorhinus cyanocephalus*) and great-tailed grackles (*Quiscalus mexicanus*), which are colonial nesting passerines, also fail to discriminate eggs. In contrast, Peer and Sealy (2000) found that great-tailed grackles possess the ability to recognize and reject some experimentally introduced conspecific eggs. Among colonial breeding waterbirds, blue petrels (*Halobaena caerulea*) appear capable of discriminating the odor of their eggs from those of conspecifics (Leclaire *et al.* 2017). However, the common pochard (*Aythya ferina*) does not recognize its own eggs from those of other species (Hořák & Klvaňa 2009). Among *Ardeidae*, egg recognition has been reported in the least bittern (*Ixobrychus exilis*), where interspecific brood parasitism by the American coot has been documented (Peer 2006). In contrast, the little bittern (*Ixobrychus minutus*), which is parasitized by the common moorhen (*Gallinula chloropus*), shows no evidence of egg discrimination (Trnka 2015). These divergent

results show that the recognition of eggs in colonial breeders merits closer attention.

Colonial breeders depend on the visual traits of own eggs or chicks to minimize confusion with neighbors and allow rapid nest recognition upon return (Buckley & Buckley 1972, Beecher 1982). In addition, high colony densities may increase the potential for CBP (Rohwer & Freeman 1989). Therefore, it is likely that birds breeding at high density in relatively homogeneous habitats have evolved some degree of individual recognition of their eggs or nestlings, although empirical evidence remains mixed. For example, Liu *et al.* (2019) found that Chinese pond herons (*Ardeola bacchus*) showed no differential preference among four types of experimental eggs, indicating a lack of egg recognition ability. Likewise, cattle egrets (*Bubulcus ibis*) respond inconsistently to foreign eggs and exhibit poor overall egg recognition abilities (Liu *et al.* 2019). The evidence from *Ardeidae* herons also illustrates this variability. González-Martín & Ruiz (1996) also recorded inter- and intraspecific brood parasitism of little egrets (*Egretta garzetta*), cattle egrets, squacco herons (*Ardeola ralloides*), and purple herons (*Ardea purpurea*), including instances of successful cross-species chick rearing (González-Martín & Ruiz 1996). In experimental clutch manipulations simulating brood parasitism, they showed that little egrets, cattle egrets, and squacco herons exhibited significantly greater nest desertion responses when the experimental egg was large rather than small. These large eggs were likely equivalent in size to the normal eggs of the focal species, suggesting that size-based cues may be sufficient to trigger rejection in some *Ardeidae* (González-Martín & Ruiz 1996). Nevertheless, species responses were heterogeneous: the stronger response to smaller eggs in squacco herons may depend on the asymmetry of the size of the host and parasitic eggs.

The little egret, a common waterbird in the order *Pelecaniformes* and family *Ardeidae* (Pang *et al.* 2020), is a tree-nesting species that breeds near wetlands and often forms dense breeding colonies, sometimes in association with the Indian pond heron (*Ardeola grayii*) (Narayanan & Vijayan 2007). Colonial breeding can increase the opportunities for brood parasitism because nests are closely spaced and readily accessible to conspecifics. Brood parasitism has been

Fig. 1. Brood parasitism experiments were conducted in the nests of the little egret. A refers to one conspecific egret egg and two host eggs during laying stage (incomplete clutch), B refers to three little egret eggs and one conspecific egg during incubation stage, C refers to two egret eggs and one quail egg during laying stage, D refers to one quail egg and three little egret eggs during incubation stage, E refers to two little egret eggs and one waterhen egg during laying stage, F refers to four little egret eggs and one waterhen egg during incubation stage, G refers to one waterhen egg and two little egret's chicks during the nestling stage, and H refers to a quail egg with host beak marks in the egret nest.

documented in several *Ardeidae* species, and experimental studies have shown that responses to foreign eggs vary among herons and egrets (González-Martín & Ruiz 1996, Liu *et al.* 2019). These findings suggest that antiparasitic defenses may not be uniformly distributed within the family and that the evolutionary relationships among colonial breeding, brood parasitism, and egg recognition remain incompletely understood. Consequently, determining whether little egrets possess egg recognition abilities can help clarify whether foreign-egg discrimination is associated with current parasitism pressure or may persist as a generalized defense in colonial *Ardeidae*.

To investigate this, we experimentally introduced a single alien egg into little egret nests and assessed host responses. Three egg types were used: conspecific little egret eggs, eggs of the white-breasted waterhen (*Amaurornis phoenicurus*), which are similar in size but differ in coloration and maculation, and eggs of the common quail (*Coturnix japonica*), which are substantially smaller and markedly different in appearance (Fig. 1). These egg types were selected to provide variations in size and appearance without mimicking host eggs. Egg size provides a readily detectable morphological cue that may facilitate discrimination of foreign eggs, particularly when size differences are large relative to host eggs (Marton *et al.* 2019, Sadam *et al.* 2026). Experimental eggs were introduced during the laying, incubation, and nestling stages to determine whether the fate of foreign eggs was influenced by egg type, clutch size, breeding stage, or the presence of an attending adult during introduction, and to test whether foreign-egg discrimination is restricted to the egg stage or persists into later breeding stages. Although isolated cases of brood parasitism and experimentally induced antiparasitic responses have been reported in little egrets from other regions (Werding 1970, González-Martín & Ruiz 1996), no such evidence is available for the present study population. Together with previous reports of generally weak or absent egg recognition abilities in other colonial *Ardeidae* (Liu *et al.* 2019), we predicted that little egrets would exhibit low but non-zero rates of foreign-egg rejection.

2. Materials and methods

2.1. Study area and species

Two breeding colonies of little egrets were located in the farmlands of the two administrative divisions: Rustam and Shahbaz Garhi, a part of the Mardan district in Khyber Pakhtunkhwa Province, Pakistan. Both divisions are in the rural section of the Mardan district (34°18′46.6″ N, 72°9′1.13″ E) and are separated by a distance of 10 km from each other. Here, irrigation is well established, and the majority of the people are either directly or indirectly engaged in farming or trading farm products (Sadam *et al.* 2022). The little egret is a medium-sized, colonial waterbird of the heron family *Ardeidae* that breeds in wetlands, marshes, lakes/reservoirs, and coastal areas. During the breeding season, they nest in colonies with dozens to hundreds of breeding pairs and are usually accompanied by other *Ardeidae* species. Nests are basic platforms made of dead twigs and are usually housed in trees or bushes. Little egrets are highly colonial breeders, often nesting at high density. For example, breeding colonies in Greece have been reported to have nest densities of 292–422 nests/ha and mean nearest-neighbor distances of approximately 1.1 m (Kazantzidis *et al.* 1997). In our study system, nests were often clustered within the same trees, with inter-nest distances typically as small as 1–2 m between neighboring breeding pairs. Such close nest proximity may increase opportunities for females to access neighboring nests, potentially facilitating brood parasitism. Little egrets lay clutches of 3–5 eggs, which are oval and blue-green (Uzun *et al.* 2008). In this study, 100 nests were monitored in 2021, and 41 nests were monitored in 2022.

2.2. Egg recognition experiment

The fieldwork was carried out from April to July (2021–2022). Nests of the little egret were identified, marked, and monitored during the breeding seasons. Each nest was sampled once to prevent repeated measurements. The experiment was not intended to simulate a specific brood-parasitism event. Instead, it tested responses to

foreign eggs that varied in size and appearance. Unlike González-Martín & Ruiz (1996), who simulated documented parasitism scenarios, we used eggs with varying similarity to host eggs. This design enabled a broader assessment of foreign-egg discrimination (Liu *et al.* 2019). Such an approach allows the evaluation of host responses across a wider range of foreign-egg characteristics. In each experimental nest, a single foreign egg was added without removing any host eggs.

Three egg types were used. Conspecific eggs were collected from active egret nests within the same colony and introduced into experimental nests without removing host eggs, with donor and recipient nests separated by approximately 5–20 m (n = 21; Fig. 1A, B). Common quail eggs were obtained from local poultry farms; these eggs were smaller and visibly distinct in color and spotting from egret eggs (n = 54; Fig. 1C, D). White-breasted waterhen eggs were collected from wild nests located outside the egret colonies; these eggs were similar in size to egret eggs but differed markedly in color and pattern (n = 66; Fig. 1E, F). The three egg types were selected to represent increasing degrees of dissimilarity relative to host eggs: conspecific eggs (similar in size and color), waterhen eggs (similar in size but different in color and pattern), and quail eggs (smaller and visually dissimilar). Differences among egg types were assessed based on morphometric measurements and human-visible characteristics; no avian visual modelling was performed.

Experimental eggs were introduced during either the egg-laying stage, when clutches were incomplete, or the incubation stage, after clutch completion. To document responses to experimentally introduced eggs after hatching, waterhen eggs were introduced into a subset of nests during the nestling period (n = 17; Fig. 1G). Only waterhen eggs were used at this stage to minimize disturbance to chicks and parental care; therefore, no conspecific control was included, and this treatment was not intended for formal comparisons among egg types or statistical evaluation of stage effects. No nest received more than one experimental egg or was subjected to repeated testing at different breeding stages. To test whether clutch size influenced rejection behavior, we recorded the number of host eggs present at the time the experimental egg was added. Clutch size was recorded at the time of egg introduction; no post-manipulation changes in clutch size were assessed. Host nests contained between two and five eggs at the time of treatment. The distribution of clutch sizes was as follows: 50 nests with two eggs, 33 nests with three eggs, 37 nests with four eggs, and 4 nests with five eggs. We also recorded whether at least one adult was present at the nest during manipulation, based on direct observation from a distance to minimize disturbance, as a proxy for immediate parental presence and potential influence on responses (Sadam *et al.* 2026).

Nests were observed for six consecutive days after eggs had been introduced, as egg rejection in birds typically occurs shortly after the appearance of a foreign egg (Antonov *et al.* 2011, Liang *et al.* 2016). An experimental egg was classified as rejected if it was removed from the nest or if it remained in the nest but showed clear beak marks consistent with pecking attempts by the host. Egg removal was categorized as rejection unless complete clutches were depredated. Accepted eggs were those that remained intact and unmarked after 6 days. Nests that were predated during the monitoring period (n = 19) were excluded from the analyses.

2.3. Statistical analysis

For each little egret nest, we averaged all host egg measurements in that nest to obtain a single value representing the egg length, width, and weight. Thus, each experimental egg (conspecific, waterhen, and quail) provided one measurement per nest, ensuring that each nest contributed a single independent observation per egg type. Egg traits were compared among egg types using a non-parametric framework because tests of normality (Shapiro-Wilk) and homogeneity of variance (Levene's test) indicated violations of ANOVA assumptions for all traits. Egg mass was cube-root transformed prior to analysis to reduce skewness and improve comparability across egg types. Differences among groups were evaluated using the Kruskal–Wallis rank-sum test. When the overall test was significant, pairwise

Table 1. Egg traits comparison among egg types: normality, homogeneity, Kruskal–Wallis tests, and post-hoc pairwise comparisons.

Trait	Shapiro–Wilk *p*	Levene's test *p*	Kruskal–Wallis H	*p*-value	Pairwise differences (Bonferroni-adjusted)
Egg length	<0.001	0.000	137.45	<0.001	Quail vs Host (<0.001); Quail vs Conspecific (<0.001); Quail vs Waterhen (<0.001); Host vs Conspecific (1.000); Host vs Waterhen (1.000); Conspecific vs Waterhen (1.000)
Egg width	<0.001	0.033	127.74	<0.001	Quail vs Host (<0.001); Quail vs Conspecific (<0.001); Quail vs Waterhen (<0.001); Host vs Waterhen (0.029); Host vs Conspecific (0.263); Conspecific vs Waterhen (1.000)
Egg weight	<0.001	0.000016	180.94	<0.001	Quail vs Host (<0.001); Quail vs Conspecific (<0.001); Quail vs Waterhen (<0.001); Conspecific vs Waterhen (0.000055); Host vs Conspecific (1.000); Host vs Waterhen (<0.001)

differences were assessed with Dunn's *post-hoc* comparisons using Bonferroni correction. As a preliminary assessment of potential pre-existing differences among females, we compared host egg length between rejector and non-rejector females using empirical cumulative distribution functions (ECDFs), which describe the proportion of observations less than or equal to each value. Analyses were performed in Python (Python Software Foundation, 2023), using pandas for data manipulation, scipy for non-parametric tests, scikit-posthocs for *post-hoc* testing, and matplotlib and seaborn for plotting box plots (Table 1; Fig. S1–S3).

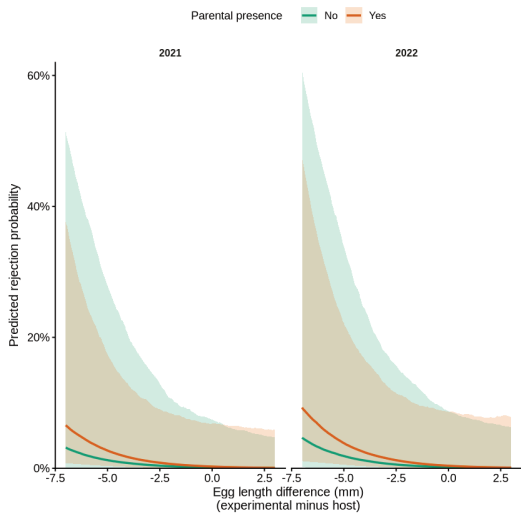

Fig. 2. Probability of rejecting the egg as a function of the difference in length between the host's own eggs and the experimental one predicted by the Bayesian-regularized logistic model. Lines indicate median posterior predictions; shaded areas correspond to 95% credible intervals. Years are plotted in panels and colored by the presence of the parent at the time the egg was added.

We tested for multicollinearity among predictor variables before modeling by examining variance inflation factors (VIF), which ranged from 1.60 to 2.46, indicating no serious collinearity issues. We used Bayesian logistic regression implemented in bayesglm (R package *arm*) to model the probability of egg rejection (1 = rejection, 0 = acceptance) as a function of egg-length difference between experimental and host eggs. Egg-length difference, used as a proxy for egg size difference, was the main predictor of interest and was calculated as the difference (mm) between the experimental egg and the mean length of host eggs within each nest. Clutch size, parental presence (yes/no), and year were included as biologically motivated covariates to account for potential variation in nesting context and sampling year; these variables were treated as control variables and were not of primary inferential interest. Given the low number of rejection events (n = 4), model estimates are necessarily uncertain and should be interpreted cautiously. The model employed the default weakly informative independent Cauchy priors used in bayesglm (Gelman *et al.* 2008), centered at zero for all regression coefficients. These correspond to Cauchy(0, 2.5) priors for slope parameters and a broader Cauchy(0, 10) prior for the intercept on the logit scale. These priors provide mild regularization, improving estimation stability in sparse-data settings and

reducing the risk of quasi-complete separation. No user-specified priors were applied. Because of the limited number of rejection events, results from this analysis are interpreted as exploratory rather than confirmatory. Model coefficients are presented as odds ratios with 95% credible intervals. Predicted probabilities and associated uncertainty were generated by simulating from the model's approximate posterior implied by the fitted coefficients and variance-covariance matrix, transforming draws through the inverse-logit to obtain median predictions and 95% credible intervals. Analysis was run in R v4.3.3 (R Core Team 2024).

3. Results

Across 141 nests, we recorded only four cases of egg rejection (2.8%). Rejection was restricted to quail eggs, whereas waterhen and conspecific eggs were always accepted. Rejection involved shell damage consistent with pecking or grasping attempts, but no eggs were completely removed. No damage was observed in any host eggs during the experiments. Females that rejected foreign eggs did not differ from non-rejectors in host egg length.

Rejection events were unevenly distributed across clutch sizes (Table 2). No rejection occurred in two-egg (n = 50) or three-egg clutches (n = 33), whereas rejection was observed only in four-egg (8.1%, n = 37) and five-egg clutches (25%, n = 4). However, sample sizes for larger clutches, particularly five-egg clutches, were small, limiting inference regarding clutch-size effects.

In the Bayesian-regularized logistic regression, the difference in egg length between experimental and host eggs had a strong negative ($\beta = -1.93$) association with rejection probability. Each 1 mm increase in egg-length difference, the odds of rejection decreased (OR = 0.63, 95% credible interval: 0.38–1.03). However, the

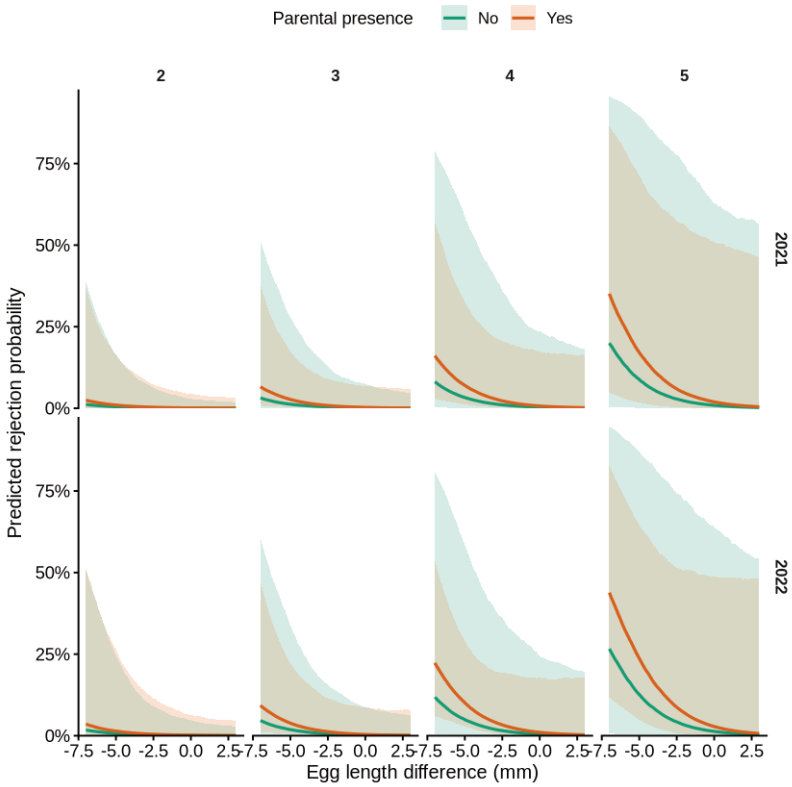

Fig. 3. Predicted probability of egg rejection as a function of differences in egg length for different clutch sizes (columns: 2–5 eggs) and years (rows: 2021 and 2022). Lines represent median posterior predictions, and shaded areas show 95% credible intervals.

Table 2. Acceptance and rejection rates of experimental eggs by little egrets in relation to clutch size.

Clutch size	Nests tested (*n* =)	Acceptance rate (%)	Rejection rate (%)
Two eggs	50	100	0.0
Three eggs	33	100	0.0
Four eggs	37	91.9	8.1
Five eggs	4	75.0	25.0

credible interval overlapped the null value (OR = 1), indicating substantial uncertainty around this effect given the few rejection events (Fig. 2).

Fig. 3 shows the model-predicted rejection probability across egg length differences, stratified by clutch size, year, and parental presence. The estimates, odds ratios, and 95% credible intervals for all predictors are provided in Table 3. Across these levels, the parameter estimates for the covariates were highly uncertain, consistent with the low number of rejection events (Table 3). The preliminary descriptive data indicated that rejection was rare and seemed to occur only in larger clutches; the model-based estimates did not provide strong statistical support for a clutch-size effect, likely due to the rarity of rejection events and uneven sample sizes across clutch categories.

Predicted rejection probabilities across the observed range of egg-length difference remained low. Median predicted probabilities decreased 1.96% at the 10th percentile (−6 mm) to 0.39% at the median (−2.5 mm) and 0.07% at the 90th percentile (1 mm), with wide 95% credible intervals reflecting the limited number of observed rejection events. Overall, these results indicate a weak tendency for lower rejection probability as experimental eggs became larger relative to host eggs, but inference remains limited by the low frequency of rejection.

4. Discussion

We experimentally tested the ability of little egrets to recognize and reject foreign eggs in breeding colonies. Rejections were infrequent and directed only at small, conspicuous quail eggs, whereas conspecific and similarly sized heterospecific eggs were always accepted. While egg length exhibited a weak and inconclusive effect on the probability of rejection, we found little support for an influence of egg traits in driving patterns of rejection behavior. Overall, the low interaction rates and universal acceptance of conspecific and similarly sized heterospecific eggs suggest an absence of specialized egg-recognition mechanisms and are more consistent with occasional nest sanitation or egg-manipulation behavior than with an adaptive

Table 3. Bayesian-regularized logistic regression estimates of predictors on egg rejection in little egrets. Values are given as log-odds, odds-ratios (OR), and their 95% credible intervals. Wide intervals indicate high sparseness in the number of rejections.

Term	Estimate	Odds ratio (OR)	95% Credible interval (OR)	Interpretation
(Intercept)	-9.78	5.68e-5	1.92e-7 – 0.017	Baseline odds of rejection when all predictors are zero. Very low, reflecting low overall rejection probability.
Egg length	-0.46	0.63	0.38 – 1.03	Main effect of interest: As experimental eggs get larger relative to host eggs, the odds of rejection decrease. Borderline significant (interval just includes 1).
Clutch size	1.03	2.80	0.71 – 11.05	Larger clutches may increase rejection odds, but the interval is wide: uncertainty is high.
Parental presence	0.78	2.18	0.08 – 62.88	Some suggest that parental presence increases rejection odds, but the extremely wide interval: not conclusive.
Year 2022	0.38	1.46	0.19 – 11.38	Slight positive effect in 2022, but again the interval is wide: inconclusive.

antiparasitic defense.

The frequency of egg rejection in little egrets was very low (2.8%), and it was only observed in quail eggs, which were smaller and visually different from their own. This minimal response indicates that little egret does not have evolved strong egg discrimination abilities. We found quite different results from those of González-Martín & Ruiz (1996), who observed that little egrets and other *Ardeidae* reacted to the artificial eggs, especially when the introduced eggs were similar to potential conspecific parasitic eggs. In contrast, rejection was rarer in our study, and eggs of similar size from conspecific and heterospecific species were always accepted. Such differences could arise from interpopulation variance, experimental design variance, or selection strength due to brood parasitism. However, egg size may influence host responses across both studies, albeit with generally weak and highly uncertain strength in our population. Egg rejection is commonly considered a costly defense that evolves under continued pressure from brood parasitism (Soler *et al.* 2011, Stoddard & Hauber 2017). Although brood parasitism seems very rare in little egrets, the overall shortage of records may limit any potential fitness advantages from having high-precision egg-recognition mechanisms (González-Martín & Ruiz 1996). Because rejection entails potential costs, including recognition errors and energetic investment, stabilizing selection may favor tolerance when parasitism risk is negligible (Lotem *et al.* 1995, Moskát & Hauber 2007, Samas *et al.* 2014, Soler 2014b). The detected increase in the incidence of rejection with increasing clutch size might be considered an evolutionary adaptation to increasing costs of potential egg loss with higher reproductive investment (Sargent 1988, Gloag *et al.* 2012, Medina *et al.* 2017). Larger clutches imply more parental effort in total, and this could favor the tighter discrimination of anomalous eggs or lower acceptance thresholds when the potential fitness cost is also higher (Davies *et al.* 1996). This pattern may indicate adaptive plasticity in host discrimination, suggesting that birds might adjust their behavior according to the costs and benefits of their current brood. Proximate cues like clutch size could signal high costs of reproduction and lead to more discrimination against atypical egg sizes or shapes (Abolins-Abols & Hauber 2020, Samaš *et al.* 2021, Dixit *et al.* 2022). Consistent with this pattern, rejection increased with clutch size in the empirical data, particularly in the largest clutches, although these estimates are based on limited sample sizes and are therefore uncertain. The Bayesian model similarly indicated a weak positive association between clutch size and rejection probability. Egg size remained a consistent cue, with smaller experimental eggs tending to be more frequently rejected or damaged. Furthermore, because a manipulation-only control was not included, we cannot completely exclude the possibility that experimental disturbance contributed to some host responses; however, the absence of rejection in the conspecific and waterhen egg treatments suggests that disturbance alone is unlikely to explain the observed pattern.

This theoretical framework is consistent with the "egg counting" hypothesis, which assumes that hosts can detect an increase in parasitic or foreign eggs by tracking clutch size; hence, a higher number of eggs exceeds the thresholds and induces rejection behavior (Lyon 2003, Wang *et al.* 2013, Guigueno *et al.* 2014). In the little egret, the lack of rejection of smaller clutches may indicate less absolute discrimination if the relative cost of mistakenly rejecting own egg exceeds the minimal risk imposed by parasitism (Abolins-Abols & Hauber 2020, Hauber *et al.* 2020). There is evidence of this mechanism from comparative cases: American coots and other species with CBP suffer higher rejection rates in larger clutches, indicating that reproductive investment drives host vigilance and discrimination efforts (Lyon 2003). Nevertheless, the rarity of rejection events and the limited sample size in larger clutches require caution in drawing firm evolutionary conclusions. The interactions observed could represent generalized nest sanitation rather than adaptive antiparasitic behavior. Other clutch size-associated traits, such as female condition or nest site quality, may also affect rejection propensity (Paasivaara *et al.* 2010, Požgayová *et al.* 2011). Overall, the observed clutch size effect in little egrets may be indicative of an adaptive, context-dependent tuning of tolerance thresholds and is consistent

with predictions from evolutionary theory models of host defense plasticity (Fasola & Pettiti 1993, Uzun *et al.* 2008). However, the low risk of parasitism and the scarcity of data on this process currently make these findings largely exploratory, and a call for ongoing experimental studies is warranted to clarify the mechanistic and evolutionary importance of clutch size in host discrimination. Future work should manipulate clutch size directly and utilize continuous video monitoring to test whether reproductive investment influences responses to foreign eggs, and to separate sanitation from actual egg discrimination.

The limited pecking and shell damage found on quail eggs in little egrets (Figure 1H) can be viewed as a form of nest sanitation, serving as an evolutionarily stable, generalist pattern to clear nests within dense colonies (Moskát *et al.* 2003, Guigueno & Sealy 2011). Although nest sanitation was not manipulated directly in this study, the preferential interaction with quail eggs suggests that little egrets respond to conspicuous visual anomalies rather than foreign eggs as targets of antiparasitic defense (Baxter 1996). In colonial breeding systems, where dense aggregations can increase the risk of pathogen transmission, ectoparasite infestation, and predation (Brown & Brown 2015, Woodworth *et al.* 2017, Kamiński *et al.* 2021), selection may favor the removal of unusual objects that could threaten nest integrity. Nest sanitation generally relies on the broad discrimination of salient stimuli rather than precise recognition, with birds often responding to unusual size, shape, or appearance instead of identifying specific object types (Li *et al.* 2021). The pecking of small, morphologically distinct quail eggs fits this pattern, whereas conspecific and similarly sized waterhen eggs were accepted. The absence of complete removal and the very low rejection frequency (2.8%) further suggest that these responses reflect generalized nest sanitation rather than evolved egg-recognition defenses against brood parasitism. Comparable patterns have been reported in other colonial or semi-colonial birds, including great reed warblers, in which nest sanitation may incidentally reduce the risk of parasitism (Moskát *et al.* 2003), pochards, which show limited foreign-egg rejection despite dense breeding conditions (Hořák & Klvaňa 2009), and cliff swallows, where nest sanitation contributes to ectoparasite control in colonial nests (Brown & Brown 1989, 2015). Moreover, nest sanitation has been proposed as a low-cost primitive behavior that may facilitate the evolution of specialized antiparasitic defenses under stronger selection pressure from brood parasitism (Yang *et al.* 2015c). In little egrets, however, where rejection appears extremely rare, nest sanitation is the most suitable explanation for the occasional manipulation of foreign eggs, including pecking directed at quail eggs without subsequent removal (Fig. 1H).

In conclusion, little egrets showed very limited foreign-egg discrimination, responding only to small and conspicuously different quail eggs while accepting conspecific and similarly sized heterospecific eggs. These results are most consistent with generalized nest sanitation rather than an evolved defense against brood parasitism. The low egg rejection rate and egg manipulation behaviors thus are better explained by generalist responses to unperceivable anomalies over adaptive defenses against parasitism. The overall pattern of higher rejection in larger clutches may indicate context-dependent variation in tolerance thresholds associated with offspring investment, although this conclusion must be considered speculative due to the infrequency of rejection. Future studies using controlled object presentations, crossed experimental designs, and continuous video monitoring will help distinguish nest sanitation from true egg discrimination and improve our understanding of object recognition in colonial waterbirds.

Yhdyskuntalintu harvoin hylkää keinomunia tai muuten reagoi niihin

Munien tunnistamista on tutkittu laajasti pesäloisjärjestelmissä, mutta sen esiintyminen ja merkitys ovat edelleen huonosti tunnettuja yhdyskunnissa pesivillä lajeilla, joilla pesäloisintaa esiintyy vähän tai ei lainkaan. Tutkimme munien tunnistamista silkkihaikaralla (*Egretta garzetta*), yhdyskunnissa pesivällä vesilinnulla, jolla pesäloisinta vaikuttaa harvinaiselta. Lisäsimme kokeessa silkkihaikaran pesiin (n = 141) saman lajin,

ojasuokanan (*Amaurornis phoenicurus*) sekä japaninviiriäisen (*Coturnix japonica*) munia ja tutkimme pesyekoon, pesinnän vaiheen ja emojen läsnäolon vaikutusta munien tunnistamiseen.

Munien hylkäämistä havaittiin vain neljässä pesässä (2,8 %), ja se kohdistui yksinomaan japaninviiriäisen muniin, jotka olivat huomattavasti pienempiä ja ulkonäöltään selvästi isäntälajin munista poikkeavia. Kaikki saman lajin ja ojasuokanan munat hyväksyttiin. Hylkäämiseen liittyi kuoren vaurioita, jotka vaikuttivat johtuvan nokkimis- tai tarttumisyrityksistä, mutta yhtään munaa ei poistettu pesästä kokonaan. Munia hylänneiden naaraiden munat eivät olleet eri kokoisia kuin niiden, jotka eivät hylänneet vieraita munia.

Bayesian-regularized logistic -mallin estimaatit viittasivat käänteiseen yhteyteen munan koon (suhteessa isäntälajin muniin) ja hylkäämistodennäköisyyden välillä, vaikka luotettavuusvälit olivat hylkäämisen harvinaisuuden vuoksi suuret. Useiden selittävien muuttujien, kuten pesyekoon, pesinnän vaiheen, emojen läsnäolon ja vuoden, vaikutukset olivat huomattavan epävarmoja. Vaikka hylkääminen vaikutti olevan yleisempää suuremmissa pesyeissä, mallin estimaatit eivät tukeneet pesyekoon vaikutusta, mikä johtui todennäköisesti tapahtumien harvinaisuudesta ja otannan epätasaisuudesta.

Kaikkiaan silkkihaikarat tunnistivat vieraat munat huonosti. Koska pesäloisintaa ei käytännössä esiinny ja munien hylkääminen on harvinaista, poikkeaviin muniin reagoiminen saattaa liittyä pikemminkin yleiseen pesän siivoamiseen tai epätavallisiin esineisiin reagoimiseen kuin kehittyneeseen pesäloisten tunnistamiseen niiden torjumiseksi.

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Author contributions. HH and WL designed this study. AS collected the data in the field, performed the analyses, and drafted the manuscript. HH and WL edited and improved the manuscript accordingly. All the authors have read and approved the final manuscript.

Ethics statement. The experiments in this study complied with the laws of Pakistan. Fieldwork was carried out with permission from the farmlands of the two tehsils (Rustam and Shahbaz Garhi). The experimental procedures were approved by the Animal Research Ethics Committee of the Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2007-001).

Data availability. Detailed egg morphometric data and supporting analyses are provided in the supplementary material (Figures S1–S3). All data supporting the findings of this study are openly available at https://doi.org/10.6084/m9.figshare.30253450 (doi: 10.6084/m9.figshare.30253450).

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Online supplementary material

Supplementary material available in the online version of the article includes Figs. S1–S3.